

Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka

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Abstract

Variation in species diversity across a landscape can be attributed to a variety of spatial and temporal factors, as well as inter-specific interactions. In this study, ant species assemblages were investigated in relation to habitat heterogeneity and tree species assemblage in a lowland dipterocarp-dominated forest in Sri Lanka. We tested the hypothesis that ant species assemblages would follow the same patterns of distribution as tree species assemblages along a small elevational gradient. A total of 100 ground-dwelling ant species and 143 tree species were recorded in 0.6 ha. Forty percent of variation in the ant species assemblages could be attributed to variation in elevation and percent plant cover at ground level. Although tree species assemblages also responded strongly to changes in elevation, there was no significant relationship between ant and tree species diversity. In this particular forest, ant species responded to the same topographical variation as did tree species assemblages; however, the ant assemblages appear to be responding to plant structure at ground level rather than to tree species diversity per se. These results suggest that preserving topographical features in a landscape may enhance ant species diversity.

Key words: Dipterocarpaceae, Forest Dynamics Plot, Formicidae, species richness, tropical rain forest.

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Introduction

The vast biological diversity found in tropical ecosystems has spawned many theories regarding the co-existence of so many species (ROSENZWEIG 1995, RICHARDS 1996, PIMM & BROWN 2004). Many studies have found that "habitat heterogeneity" or "habitat diversity" can determine animal diversity. TEWS & al. (2004) reviewed 85 publications and found that 85% of the studies showed positive relationships between animal species diversity and measures of vegetation structure. However, more recent studies in temperate regions have shown that tree species assemblage can better predict animal assemblages in a given area (TER BRAAK & SCHAFFERS 2004). Tree species can directly influence animal diversity by providing food and substrate resources, and indirectly by affecting light availability and microclimate (PALIK & ENGSTROM 1999). In terms of ground-dwelling arthropods, tree species determine the quality and density of litter (by the periodicity and synchronicity of leaf fall) (BURGHOUTS & al. 1994) and provide food resources such as seeds (LEVEY & BYRNE 1993) and nectar (DEJEAN 1991). However, the relative contributions of plant species diversity and vegetation structure to animal species richness in tropical forests are still not well understood (RICHARDS 1996).

A number of mechanisms may contribute to the patchy spatial distribution of ant species, especially in tropical ecosystems (LEVINGS & FRANKS 1982, KASPARI 1996). RIBAS

& SCHOEREDER (2007) found that tree density and structural heterogeneity affected ant species composition and that increased structural heterogeneity led to increased ant species richness. Others have found ant species distributions were related to the quantity and weight of leaf litter (THEUNIS & al. 2005) and to local topography (CATTERALL & al. 2001, VASCONCELOS & al. 2003).

In this study, we analysed ant species assemblages in relation to measured environmental variables, as well as understorey vegetation structure in a lowland tropical rainforest in southwestern Sri Lanka. We hypothesized that ground-dwelling ant species will also demonstrate distinct patterns of distribution along a small slope and these patterns would follow changes in the vegetation structure at ground level. However, the existence of tree species data also gave us the opportunity to analyse whether ant species distribution could also be explained by tree species assemblages directly within a small section of lowland tropical wet forest.

Materials and methods

Study Site: The Sinharaja Forest Dynamics Plot (FDP) was set up in 1993 within the 11,000 ha Sinharaja Forest Reserve (SFR), a UNESCO World Heritage Site in southwestern Sri Lanka (6° 21' - 26' N, 80° 21' - 34' E; GUNATILLEKE & al. 2004b). The dominant vegetation is a mixed dipterocarp

(*Mesua-Shorea* type), lowland, wet forest and it receives 4000 - 5000 mm of rain annually, with no period where the average monthly rainfall drops below 60 mm. The forest receives monsoonal rain from May to June (south-west monsoon) and from September to November (north-east monsoon), resulting in higher rainfall in these two periods.

Common tree species across the FDP in the SFR exhibit a number of non-random spatial patterns (GUNATILLEKE & al. 2006). Species of the dipterocarp genus *Shorea* are distinctly distributed within the plot, with one species, *Shorea megistophylla* (ASHTON), colonising only ridge-top areas. The most abundant understorey tree, the myrmecophytic *Humboldtia laurifolia* (VAHL), is also restricted to higher-elevation areas, mainly on spurs within the plot. Soil moisture and nutrient content have been implicated as possible drivers for these patterns (GUNATILLEKE & al. 2004a).

Ant sampling: The FDP measures 500 × 500 m and was laid out in undisturbed forest in the western portion of the reserve (6° 24' N, 80° 24' E; Fig. 1). The topography of the FDP is highly variable, with a central valley containing a small stream and an elevation range of 424 - 575 m; the largest range in elevation is found on the south-west-facing slope (GUNATILLEKE & al. 2006). The FDP is divided into 625 quadrats 20 × 20 m in size. Every tree greater than 1 cm in diameter at breast height (dbh) has been tagged, identified, and measured (see MANOKARAN & al. (1990) and CONDIT (1995) for further details). The ant collections were carried out in the northern quarter of the FDP, along its south-west facing slope. Only a small section of the plot was surveyed in order to ensure that all sites had the same aspect.

Plots were located along three parallel 200-m transects spaced 50 m apart on the south-west-facing slope. Ants were collected in five 10 × 10-m plots per transect (a total of 15 plots), centred within the larger 20 × 20-m FDP quadrat. Each plot was spaced 30 m apart along each transect in an area where elevation ranged from 400 m to 600 m. Placement of plots further apart was restricted by changing slope and aspect within the FDP. All fieldwork was carried out during four collection periods two to three months apart, in 2006. This high-intensity sampling was done so as to eliminate potential effects of variable rainfall, as moisture availability has been shown to affect ant species activity, even in tropical wet forests (KASPARI & WEISER 2000).

Ants were sampled using two established methods for invertebrate collection: Winkler extraction and pitfall trapping (BESTELMEYER & al. 2000). In each plot, four leaf-litter collections and four pitfall traps were set out to maximise the number of leaf-litter ants collected. Leaf litter was collected in a 1 × 1-m quadrat and was sifted using a Winkler litter sifter. The sifted material was then hung inside a Winkler sack for 48 h, with the leaf litter being removed and shaken after the first 24 h.

Each pitfall trap consisted of two nested plastic drinking cups (mouth diameter 8 cm) which were inserted into the ground and left for one week before being filled with ~ 70 ml of methylated spirits. Each trap was then capped with another inverted plastic cup with large triangles cut out of the sides to provide a lid that prevented rainfall from flooding the cup. After 72 h, the material in the inner cup was collected, and the outer cup was filled with leaf litter and left in the ground. Litter was removed at subse-

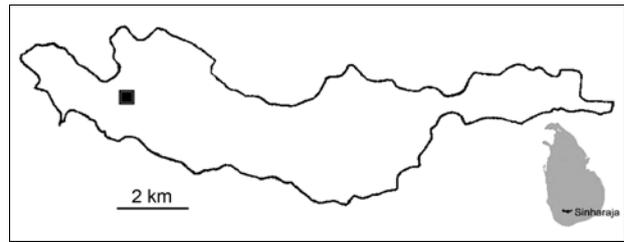


Fig. 1: The 25-ha Forest Dynamics Plot (black box), located in the western portion of Sinharaja Forest Reserve in Sri Lanka (inset).

quent sampling periods and a fresh cup inserted. The collected material was washed with ethanol and returned to the laboratory.

All invertebrates were removed from the Winkler and pitfall samples and stored in 70% ethanol. The ants were subsequently separated from the invertebrate material and point-mounted and identified to morphospecies. Once a reference collection of point-mounted specimens was created, all excess ants were stored in 80% ethanol. Ants were identified to species whenever possible, with certain genera being sent to specialists for confirmation of species. The wet and dry specimens are housed in Peradeniya University Entomology Museum and a mounted voucher collection is stored in the Curtin University Entomology Museum.

Statistical analysis: For each plot, the ant data from the four pitfall traps and the four leaf-litter samples were combined. The data from each collection period were then combined for each of the 15 plots. There were no significant differences in ant species richness and assemblages between collection periods when data from both collection methods were combined (GUNAWARDENE & al. 2008). The combined data from the four seasons were then assessed for collection effort and the completeness of the species assemblage by using species richness estimators. This analysis was carried out using EstimateS (COLWELL 2009) using three established species richness estimators, Chao 2, Jack1 and Bootstrap. These species richness estimates generated can be a useful lower bound estimation of actual species richness in an area (GOTELLI & COLWELL 2001).

Ant species for which only one individual was collected in the whole study (singletons) were then eliminated from the matrix. This is done as it has been shown that rare species or singletons in a dataset do not necessarily contribute further information for understanding patterns in species ordinations (AUSTIN & GREIG-SMITH 1968). Ants are social insects and tend to be aggregated in space and time (LONGINO 2000), which may affect abundance data analyses, since some methods, particularly litter sampling methods, would most likely have captured entire colonies. For this reason, the data were then converted into a presence / absence matrix.

Four readings of air temperature (1 m above ground level) and relative humidity (1 m above ground level and at ground level) were recorded in each plot using a Centre[®] 310 RS-232 humidity / temperature meter. Four readings of insolation at ground level were recorded using a TPS[®] MC-88 digital light meter. These four readings were averaged for each plot within each collection period. Elevation was recorded at the centre of each plot using Garmin GPS unit and cross referencing to a survey map of the area.

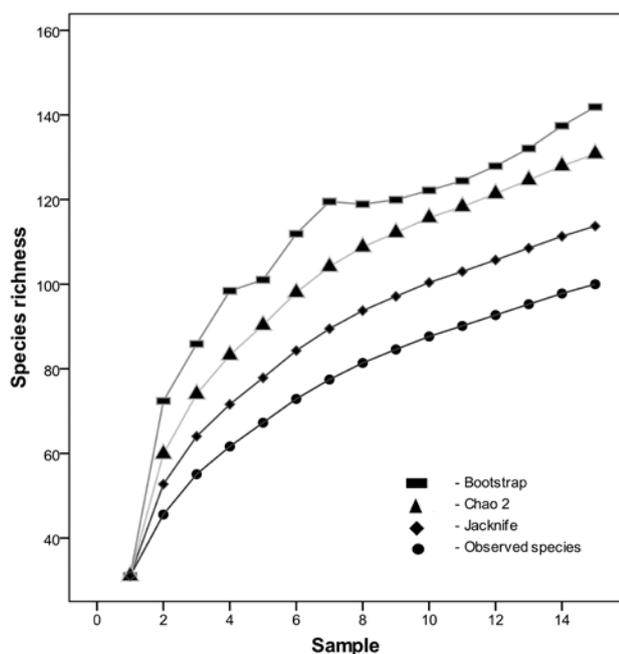


Fig. 2: Species richness curves for ant species in Sinharaja Forest Dynamics Plot sample area, indicating that there is some levelling of species accumulation. The circles represent observed species richness (100 species), diamonds indicate bootstrap species richness estimates, triangles represent jack-knife (Jack1) estimates, and rectangles indicate Chao2 results. A further 14, 30 and 42 species (bootstrap, jack-knife and Chao2 estimates respectively) are estimated to occur in this part of the forest.

Ground cover characteristics of each plot were quantified by estimating the percentage coverage by bare ground, leaf litter, large rocks, and plant stems in a 1-m² quadrat. Also, in the same quadrat, the number of dead branches and tree trunks (> 10 cm) were recorded and the depth of the leaf litter was measured using a ruler. Four quadrats were measured in each plot in each collection period and the resulting data averaged.

Canopy cover was estimated using a GRS[®] densitometer at 40 points within each plot in each collection period. Understorey foliage density was also estimated using a Levy pole (LEVY & MADDEN 1933, MAJER 1981), with readings taken at four points within each plot. The pole was divided into four intervals: 0 (ground) - 50 cm, 51 - 100 cm, 101 - 150 cm, and 151 - 200 cm. The number of points where the pole was touched by vegetation was counted. At each interval, the number of plant touches for each of the four recordings was summed and divided by the 16 recordings taken for the plot over the course of the collection period.

Tree species data were taken from the 2002 census data made available by S. and N. Gunatilleke. Tree species diversity was measured as the total number of species present in each FDP quadrat within which ants were collected. Total dbh in each quadrat was also calculated as a variable. Tree species density was measured as the total number of stems per species per FDP quadrat.

All environmental variables were individually correlated with every other variable using Pearson Correlation and those variables that were highly correlated were re-

moved from the group ($P < 0.05$). This was done so as to reduce the effect of collinearity within the multiple variables. The remaining variables, ant species richness and tree species richness, were then $\log(x + 1)$ transformed to reduce variance prior to analysis. The relationship between ant species composition in plots was assessed using a Bray-Curtis dissimilarity measure (KRUSKAL 1964). The ant species assemblage was then analysed with the remaining non-collinear environmental variables using the multivariate regression procedure, DISTLM (distance-based linear models) (ANDERSON 2001, MCARDLE & ANDERSON 2001). The best fit selection procedure was utilised (using AIC model selection criterion) to determine which variables best explained the variation in species assemblages. The model with the best predictors was fitted against a distance-based redundancy analysis (dbRDA) (LEGENDRE & ANDERSON 1999, MCARDLE & ANDERSON 2001), which performs a constrained ordination of sample sites using the same Bray-Curtis dissimilarity matrices of ant and tree data. DISTLM and dbRDA procedures were run using Primer v.6.1.9.

Relating ant species assemblages to tree species assemblages was carried out using a relatively new method, co-correspondence analysis (CoCA) (TER BRAAK & SCHAFFERS 2004). This method measures the covariance between weighted averages species scores of one assemblage with the weighted averages species scores of another assemblage. It uses a partial least squares (MARTENS & NAES 1992) analysis to predict species composition of one set of organisms from another set of organisms and then compares the predicted species composition with the actual species composition. The method uses a "leave-one-out" cross-validation of sites to obtain a cross-validatory fit of the model. This is calculated as $100 \times (1 - ssp_a / ssp_o)$, with ssp_a being the sum of squared prediction errors of the model and ssp_o the sum of squared prediction errors under the null model of no relationship (SCHAFFERS & al. 2008). It has been suggested that any value greater than 0 % fit for the model is a validation in itself for the prediction, as any value above zero indicates that the prediction is better than what could have occurred as a result of pure chance (GIORIA & al. 2010). As abundances are used in this analysis, tree species stem density was used as a predictor for ant species abundance (response variable). The CoCA analysis was carried out using the "cocorresp" package within the R statistical program (SIMPSON 2005, R DEVELOPMENT CORE TEAM 2006).

Results

A total of 100 ground-dwelling ant species were collected in 0.6 ha of forest within the FDP of Sinharaja (Tab. 1). Species richness estimates indicate there could be between 14 and 42 more species that could be collected in the FDP (Fig. 2). The trajectory of the observed species richness curve does indicate that it may eventually reach an asymptote with greater sampling effort. The most abundant ants in the FDP were *Paratrechina* sp. SL001, *Technomyrmex bicolor* (EMERY, 1893), *Aneuretus simoni* (EMERY, 1893) and *Tetramorium* sp. SL002 which were also among the most commonly occurring ants. There were 27 ant species that were represented by one specimen (singletons) and 33 that were unique to one plot.

A total of 143 tree species [out of 205 tree species and 10 liana species (GUNATILLEKE & al. 2006)] were present

Tab. 1: List of the 100 ant species collected in the Sinharaja Forest Dynamics Plot over four collection periods. The table also shows the occurrence of each species across the 15 plots in three parallel transects (1, 2 and 3 going down the slope), as well as the total abundance of each species from all four collection periods combined. N.R. Gunawardene used keys in BOLTON (1994) for genus level identification and then designated morphospecies numbers to each species. Species were then determined (by N.R. Gunawardene), where possible, by using specific taxonomic publications or were sent to a taxonomic specialist as indicated in the final column.

Subfamily	Genus and Species	Total	1-1	1-2	1-3	1-4	1-5	2-1	2-2	2-3	2-4	2-5	3-1	3-2	3-3	3-4	3-5	Keys used / taxonomist	
Aenictinae	<i>Aenictus binghami</i> FOREL, 1900	1			*													T. Varghese	
	<i>Aenictus</i> nr. <i>punensis</i> FOREL, 1901	1					*											BINGHAM (1903)	
Aneuretinae	<i>Aneuretus simoni</i> EMERY, 1893	620	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	BINGHAM (1903)	
Cerapachyiinae	<i>Cerapachys</i> sp. <i>dohertyi</i> gp. SL106	6							*		*						*	P. Ward	
	<i>Cerapachys</i> sp. <i>dohertyi</i> gp. <i>sulcinodis</i> (<i>risii</i>) EMERY, 1889	9	*														*	P. Ward	
	<i>Cerapachys luteoviger</i> BROWN, 1975	5												*				P. Ward	
	<i>Cerapachys</i> sp. <i>dohertyi</i> gp. SL104	1	*															P. Ward	
	<i>Cerapachys</i> sp. <i>dohertyi</i> gp. SL165	1															*	P. Ward	
	<i>Cerapachys typhlus</i> (ROGER, 1861)	1															*	M. Borowiec	
Dolichoderinae	<i>Dolichoderus</i> sp. SL089	1			*														
	<i>Tapinoma</i> sp. SL147	2		*							*								
	<i>Technomyrmex bicolor</i> EMERY, 1893	682	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	BINGHAM (1903)	
	<i>Technomyrmex albipes</i> (Fr. SMITH, 1861)	217	*		*	*	*	*	*	*	*	*	*	*	*	*	*	BINGHAM (1903)	
Ectatomminae	<i>Gnamptogenys coxalis</i> gp. sp. nr. <i>binghami</i> FOREL, 1900	1										*						LATTKE (2004)	
Formicinae	<i>Acropyga</i> sp. SL093	1													*				
	<i>Camponotus</i> cf. <i>irritans pallidus</i> SMITH, 1857	4						*							*		*	BINGHAM (1903)	
	<i>Camponotus</i> cf. <i>angusticollis</i> (JERDON, 1851)	2					*				*							BINGHAM (1903)	
	<i>Camponotus</i> sp. SL169	1								*									
	<i>Camponotus</i> sp. SL172	1									*								
	<i>Myrmoteris binghami</i> FOREL, 1893	6													*	*	*	BINGHAM (1903)	
	<i>Paraparatrechina</i> nr. <i>bourbonica</i> (FOREL, 1886)	723	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	R. Taylor
	<i>Paraparatrechina</i> sp. SL036	220		*		*	*	*	*			*	*	*		*	*		
	<i>Paraparatrechina minutula</i> (FOREL, 1901)	4						*		*			*					S. Shattuck	
	<i>Polyrhachis (Hemioptica) bugnioni</i> FOREL, 1908	2										*						R. Kohout	
<i>Pseudolasius familiaris</i> (SMITH, 1860)	14				*												BINGHAM (1903)		
Leptanillinae	<i>Protanilla</i> sp. SL129	14								*			*						
Myrmicinae	<i>Carebara (Oligomyrmex)</i> sp. SL012	109		*	*	*	*	*	*	*	*	*	*	*	*	*	*		
	<i>Crematogaster</i> cf. <i>biroi</i> MAYR, 1897	13		*	*						*							K. Ogata	
	<i>Crematogaster</i> cf. <i>soror</i> FOREL, 1902	1														*		K. Ogata	
	<i>Crematogaster</i> cf. <i>wroughtoni</i> FOREL, 1902	1				*												K. Ogata	
	<i>Monomorium</i> cf. <i>floricola</i> (JERDON, 1851)	71	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	B. Heterick	
	<i>Monomorium destructor</i> gp. SL137	51	*	*				*	*	*		*					*	B. Heterick	
	<i>Monomorium hildebrandi</i> gp. cf. <i>australicum</i> FOREL, 1907	101				*	*						*		*	*	*	B. Heterick	
	<i>Monomorium floricola</i> (JERDON, 1851)	1									*							B. Heterick	
	<i>Myrmecaria brunnea</i> SAUNDERS, 1842	33	*	*	*	*	*				*							B. Yahya	
	<i>Myrmecaria</i> sp. A	1															*	B. Yahya	
	<i>Pheidole</i> sp. SL027	39		*	*			*	*	*	*	*	*	*	*	*	*	*	
	<i>Pheidole</i> sp. SL028	62		*	*	*	*		*				*	*	*	*	*	*	
	<i>Pheidole</i> sp. SL142	53	*	*		*	*	*				*	*	*			*	*	
	<i>Pheidole</i> sp. SL030	216			*	*	*				*	*	*	*			*	*	

Ponerinae	<i>Hypoponera</i> sp. SL114	5										*	*					
	<i>Hypoponera</i> sp. SL066	1											*					
	<i>Leptogenys processionalis</i> (JERDON, 1851)	49	*	*		*	*	*	*				*	*				T. Varghese
	<i>Leptogenys</i> nr. <i>diminuta</i> (SMITH, 1857)	31				*				*								T. Varghese
	<i>Leptogenys</i> sp. SL072	6				*		*										
	<i>Leptogenys</i> cf. <i>moelleri</i> (BINGHAM, 1903)	1			*													T. Varghese
	<i>Pachycondyla</i> (<i>Mesoponera</i>) <i>melanaria</i> (EMERY, 1893)	6			*	*				*		*		*				T. Varghese
	<i>Pachycondyla</i> (<i>Bothroponera</i>) <i>sulcata</i> FRAUENFELD, 1867	23							*	*					*	*		T. Varghese
	<i>Pachycondyla</i> (<i>Bothroponera</i>) <i>rufipes</i> JERDON, 1851	6	*			*			*		*							T. Varghese
	<i>Ponera</i> cf. <i>truncata</i> SMITH, 1860	5		*		*	*	*										BINGHAM (1903)
	<i>Ponera</i> cf. <i>gleadowi</i> FOREL, 1895	2										*	*					T. Varghese
Pseudomyrmecinae	<i>Tetraponera attenuata</i> F. SMITH, 1877	3				*	*	*										WARD (2001)

Tab. 2: Ant species richness and total ant abundance displayed together with the environmental variables and tree species variables for each of the 15 plots within three parallel transects (1, 2 and 3 going down-slope) in the Sinharaja Forest Dynamics Plot. Environmental variables were averaged over the four collection periods and tree species variables included the total no. of stems, the no. of tree species, as well as the total dbh in each plot.

Site / variable	1 - 1	1 - 2	1 - 3	1 - 4	1 - 5	2 - 1	2 - 2	2 - 3	2 - 4	2 - 5	3 - 1	3 - 2	3 - 3	3 - 4	3 - 5
Temperature °C	23.37	24.13	24.24	24.93	25.13	24.85	24.26	25.04	25.27	25.73	24.55	24.94	25.02	26.18	26.50
Relative humidity, soil	100.00	99.47	99.13	99.55	99.98	100.00	97.83	96.80	98.00	96.49	100.00	100.00	100.00	100.00	100.00
Relative humidity, air	98.97	96.58	97.34	97.32	98.69	98.22	96.19	95.09	96.89	94.35	100.00	88.75	98.33	99.13	96.80
Insolation	34.63	32.88	32.50	39.88	31.38	41.38	29.25	53.88	57.25	48.25	57.50	75.75	48.13	128.75	99.75
Elevation (m)	565	565	565	575	575	495	505	505	505	495	435	435	445	435	435
% bare ground	0.31	5.00	5.94	0.63	0.00	1.56	13.44	2.81	25.94	14.69	3.13	12.81	1.56	0.00	4.38
% litter cover	99.06	87.19	91.81	95.63	93.44	88.44	84.06	94.38	56.25	82.19	82.81	83.44	98.13	93.75	83.75
% stone cover	0.00	6.56	2.19	0.00	0.00	8.13	0.94	0.00	10.31	3.13	3.13	2.19	0.00	0.31	9.38
% plant cover	0.63	1.25	0.06	6.00	6.56	1.25	1.56	2.19	2.19	0.00	4.69	1.56	0.31	5.94	2.50
No. of branches	0.50	0.25	0.56	0.06	0.06	0.06	0.06	0.06	0.00	0.63	0.06	0.00	0.25	0.06	0.44
Litter depth	2.02	2.25	1.91	2.46	1.88	1.28	1.25	1.77	1.18	0.89	1.07	1.44	1.33	1.55	1.36
Canopy cover	94.38	91.88	93.75	98.13	97.50	93.75	100.00	100.00	96.88	86.88	90.63	92.50	99.38	86.88	88.75
Foliage density 0 - 50	0.00	1.56	4.69	6.25	0.00	10.94	1.56	6.25	10.94	14.06	9.38	6.25	12.50	20.31	20.31
Foliage density 51 - 100	6.25	4.69	6.25	1.56	1.56	4.69	1.56	4.69	7.81	1.56	9.38	1.56	3.13	3.13	6.25
Foliage density 101 - 150	3.13	4.69	1.56	4.69	1.56	0.00	7.81	12.50	1.56	4.69	3.13	4.69	3.13	3.13	1.56
Foliage density 151 - 200	4.69	1.56	4.69	4.69	3.13	6.25	3.13	7.81	1.56	9.38	6.25	3.13	4.69	4.69	1.56
No. of stems	172	296	265	419	422	246	247	333	107	277	136	155	210	160	158
No. of tree species	25	34	25	43	44	30	37	34	29	43	42	35	54	37	42
Total dbh	1285.85	1070.94	2406.00	2311.88	2252.20	2227.63	1410.62	1112.51	2335.25	1635.55	3431.83	1694.10	3794.16	2117.93	2098.07
No. of ant species	29	30	28	35	37	31	31	29	32	31	39	29	28	29	32
Abundance of ants	272	253	308	499	435	306	210	364	217	316	521	266	259	219	381

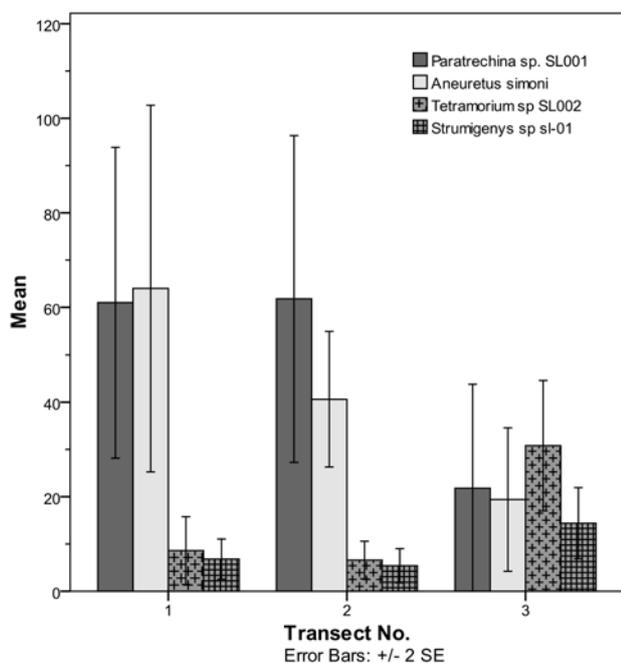


Fig. 3: Mean abundances (with standard error bars) of four of the more numerous ant species collected in the three parallel transects (1, 2 and 3 going down-slope) within the Sinharaja Forest Dynamics Plot. Overall, these ant species show general trends of increasing abundances in the higher elevations (*Aneuretus simoni* and *Paratrechina* sp. SL001) or in the lower elevations (*Tetramorium* sp. SL002 and *Strumigenys* sp. sl-01).

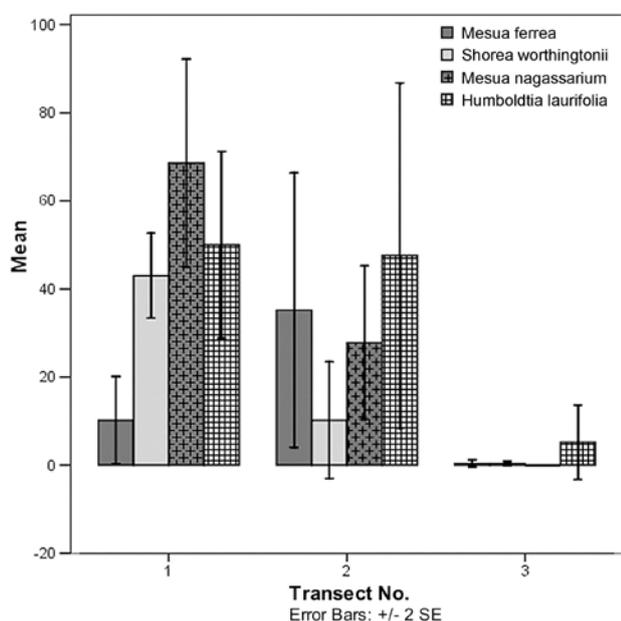


Fig. 4: Mean tree stem densities (with standard error bars) for the four tree species having the greatest number of stems in the study area within the Sinharaja Forest Dynamics Plot. The data were collated for the three parallel transects (1, 2 and 3 going down-slope). Three of the four tree species (both *Mesua* species and the *Shorea* species) are large canopy emergents, while *Humboldtia laurifolia* is an understorey tree. Three species are more abundant in the higher elevations, although *Mesua ferrea* is most abundant mid-slope, but also abundant at the higher elevations.

Tab. 3: Distance-based linear modelling (DISTLM) of ant species assemblage with non-collinear environmental variables, demonstrating that only foliage density at 0 - 50 cm and elevation were significant at the $P < 0.05$ level. The environmental variables analysed were per cent stone cover (stone), per cent plant cover (plant), litter depth (Litter D), foliage density at 0 - 50 cm, 51 - 100 cm, 101 - 150 cm, 151 - 200 cm, total number of tree species per quadrat, and elevation. Prop represents the proportion of variation explained by each variable.

Variable	Sum of squares (trace)	Pseudo-F	P	Prop.
stone	688.7	0.84259	0.612	6.09E - 02
plant	1321.2	1.7188	0.063	0.11678
Litter D	1179.3	1.5126	0.138	0.10423
0 - 50	1839.9	2.5246	0.003	0.16262
51 - 100	758.71	0.9344	0.53	6.71E - 02
101 - 150	576.7	0.6982	0.742	5.10E - 02
151 - 200	854.11	1.0615	0.408	7.55E - 02
No. of tree species	1273.8	1.6493	0.08	0.11259
Elevation	1877.3	2.586	0.002	0.16592

in the 15 quadrats analysed in the study. The most widespread tree species (found in all 15 quadrats) were *Myristica dactyloides* (GAERTN) (a canopy tree) and *Garcinia hermonii* (KOSTERM) (an endemic understorey tree). However, *H. laurifolia* (a myrmecophytic understorey tree) and *Mesua nagassarium* (KOSTERM) (a canopy tree) had the highest stem densities, mostly in the upper two transects.

The total abundances at each plot for four of the more abundant ants in the study show a general trend of higher abundances in either high or low elevation (Fig. 3). This is similarly reflected in tree species with high stem densities (Fig. 4). These graphs display the differences in abundances from low- to high-elevation plots.

Elevation was highly correlated with all the physical variables (temperature, humidity and insolation) and was used as a surrogate for these variables (Tab. 2). Hence, the final non-collinear environmental variables tested were elevation, per cent stone cover, per cent plant cover, litter depth, foliage density at 0 - 50 cm, 51 - 100 cm, 101 - 150 cm, 151 - 200 cm and total number of tree species per quadrat.

According to the DISTLM analysis, only two variables were significantly associated with ant assemblages, namely elevation (Pseudo F = 2.59, P = 0.002) and foliage density 0 - 50 cm (Pseudo F = 2.52, P = 0.003) (Tab. 3). The first two axes of the dbRDA (Fig. 5) adequately displayed 53.5% of the model fitted with the nine variables, and explained 39% of the total variation of the ant species data. The dbRDA plot shows, to some extent, a separation of upper-elevation and lower-elevation plots. It also shows the influence of elevation on the upper elevation sites and foliage density towards the lower-elevation sites.

As a comparison, the tree species matrix was run against the same environmental variables and ant species richness using the same methods as for the ant species matrix (see Appendix 1 and 2, as digital supplementary material to this article in the journal's web pages). The first two axes ex-

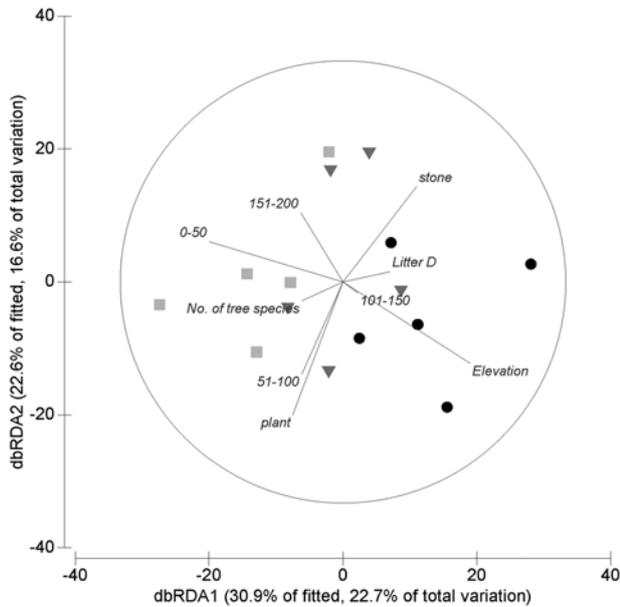


Fig. 5: Distance-based redundancy analysis (dbRDA) utilizing a Bray-Curtis dissimilarity matrix based on ant species presence / absence. The ordination shows 15 plots (five plots along three parallel transects going down a slope: 1 = ●; 2 = ▼; and 3 = ■); and the influence of seven non-collinear variables: per cent stone cover (stone); per cent plant cover (plant); litter depth (Litter D); foliage density at 0 - 50 cm, 51 - 100 cm, 101 - 150 cm, 151 - 200 cm; and number of tree species per quadrat and elevation.

plained up to 62% of the fitted model and 49% of the tree species variation. The same two variables as the ant matrix were significant for tree species as well, namely elevation (Pseudo $F = 6.45$, $P = 0.001$) and foliage density 0 - 50 cm (Pseudo $F = 3.12$, $P = 0.019$).

The first two axes of the predictive Co-CA showed that up to 20% of the ant species (response) could be predicted by the tree species (predictor). However, the results of the multiple permutation tests carried out to assess the PLS components showed that only the first axis was significantly associated ($P = 0.01$), and all subsequent axes were not ($P > 0.33$). Even running the Co-CA as a symmetric model to assess the relative effects of the tree species assemblage on ant species and vice versa, did not yield more than one significant axis. Hence, the null model cannot be disproven.

Discussion

For terrestrial animals and plants, major changes in elevation are often associated with changes in species distribution and diversity (HODKINSON 2005). However, in this study, even a small change in elevation (> 200 m) was associated with changes in ant species. Together with per cent cover of plants on the ground, ant species appeared to be responding more to small elevation change rather than directly to tree species richness. These two variables account for almost 40% of the variation in the ant fauna, whereas direct comparisons of ant and tree species assemblages did not yield any support for either dataset influencing the distribution of the other.

Intuitively, the tree species (also influenced by elevation) would determine the plant-associated cover on the ground by creating the appropriate microhabitat for the un-

derstorey to thrive. However, a recent study on litter arthropod diversity in tropical forest failed to find a relationship between tree species and their associated litter structural heterogeneity (DONOSO & al. 2010). It is possible that underlying physical factors, such as elevation, change the degree to which tree species can create a predictable litter habitat. Hence, environmental variables, such as plant cover and other ground-level characteristics, are better determinants of ant species distribution than tree species composition.

In terms of changes in elevation across a slope, VASCONCELOS & al. (2003) found greater ant species richness in valleys compared to plateaux in Amazonian forest, where ants are potentially tracking moisture gradients (KASPARI & WEISER 2000). CATTERALL & al. (2001) found greater abundances and more characteristic species assemblages in a variety of taxa, including ants, in riparian sites compared to sites 15 - 35 m higher up along a slope in subtropical eucalypt forest. They suggested that riparian habitats would be characterised by higher moisture availability, hence affecting the vegetation and litter dynamics. However, in this study, there were generally fewer ant species and individuals in the low-elevation plots. The low-elevation plots were adjacent to a permanent stream that traversed the valley bottom in the FDP. Two of the main drainage lines flowed through the collection area, emptying into the stream. During the collection period, there was a noticeable increase in water flow in the drainage lines and an increase in soil inundation in the lower plots (N.R. Gunawardene, unpubl.). Soil inundation has been shown to affect ant nesting and to reduce species diversity and abundance (MAJER & DELABIE 1994, BALLINGER & al. 2007). GUNATILLEKE & al. (2006) have observed greater cover of herbaceous species in lower-elevation areas compared to woody species. They have also documented lower mean stem density and basal area compared to upper-elevation sites.

The presence of large canopy gaps in the lower elevation, where trees have died off in large clumps (N. Gunatilleke, unpubl.), may also have had an effect on ant species composition. Variable light conditions in canopy gaps alter plant community composition (DENSLOW 1987) and hence the invertebrate community that is dependent upon them. Ant assemblages in gaps appear to be more sensitive to seasonal variation in abiotic conditions (FEENER & SCHUPP 1998), as are other arthropod groups (RICHARDS & WINDSOR 2007). This may have contributed to differentiating the species composition of the lower plots from the upper plots.

According to the ordination, 60% of the variation in the ant species assemblage was not explained by the vegetation variables. Other aspects of topography may explain more of the variation in the ant assemblages, but the current study was limited by the number of plots analysed, making the dataset less robust to further analyses. Future studies should sample plots with a different aspect, using both collection methods.

Species richness estimators are influenced by singletons in a dataset and the species richness estimators used here indicate that up to 40% more ant species could be collected in this area of the forest. GUNAWARDENE & al. (2010) found that similar numbers of singletons occurred in logged forest and higher elevation unlogged forest plots in the Sinharaja Forest Reserve. The 25 singleton ant species that were excluded from the analysis may provide further in-

sight into the habitat relationships within the FDP. Analysis of arboreal and shrub-dwelling ants may also reveal clearer trends in terms of the relationship to tree species distribution. WILKIE & al. (2010) found that up to 80% of ant species were confined to only one stratum of Ecuadorian rain forest, which could indicate that the ground-dwelling ants respond to different environmental indicators compared to arboreal ants. RIBAS & al. (2003) found significant relationships between arboreal ant species richness and tree species and tree density in Brazilian cerrado. It would be of interest to compare the singleton species group from each forest type to see if there were any similarities in the rare species in different parts of the forest and whether there would be any justification in leaving some of the singletons within the dataset.

Overall topographical changes, and the associated shifts in vegetation structure at ground level from valley bottom to ridge top, can significantly alter ant species composition. Sheltered, upper-elevation gullies can support high species richness and can potentially act as harbours of ant diversity in tropical forests in Sri Lanka. Conservation of forest fragments in south-west Sri Lanka with high topographical variation has the potential to protect a large proportion of ant species richness found in the country.

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